What Did the Ancestors of the Woodroach *Cryptocercus* Look Like? A Phylogenetic Study of the Origin of Subsociality in the Subfamily Polyphaginae (Dictyoptera, Blattaria)

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ABSTRACT

Studies of relationships between *Cryptocercus* and termites have been biased because of the use of the misleading concept of "primitive taxon". Using the phylogeny of the subfamily Polyphaginae (including *Cryptocercus*), the traits ancestral to *Cryptocercus* and its sister-genus have been inferred. *Cryptocercus* appeared from an ancestor distributed in tropical forests of Indo-Asia, inhabiting treeholes or holes in termite nests, being gregarious and displaying an alarm behavior involving disruptive coloration of wings and pleural gland. The pattern of change from ancestral gregariousness toward derived subsociality in the case of *Cryptocercus* provides indications *by analogy* for a modification of the theories of social evolution in termites.

RÉSUMÉ

A quoi ressemblaient les ancêtres de la blatte xylicole *Cryptocercus*? Une étude phylogénétique de l'origine de la subsocialité dans la sous-famille des Polyphaginae (Dictyoptera, Blattaria)

Les recherches entreprises à propos des relations entre la blatte *Cryptocercus* et les termites ont été longtemps biaisées à cause de l'utilisation du concept erroné du « taxon primitif ». Avec l'analyse phylogénétique de la sous-famille des Polyphaginae (incluant *Cryptocercus*), il est possible de retracer les caractéristiques ancestrales à *Cryptocercus* et à son genre-frère. *Cryptocercus* s'est diversifié à partir d'un ancêtre vivant dans les forêts tropicales d'Inde et d'Asie, qui habitait les troncs creux ou les termitières creuses, était grégaire et montrait un comportement d'alarme mettant en jeu une coloration disruptive et une glande pleurale. L'hypothèse d'un passage d'un grégarisme ancestral à la subsocialité dérivée dans le cas de *Cryptocercus* permet de proposer *par analogie* des modifications aux théories sur l'évolution de la socialité chez les termites.

INTRODUCTION

An understanding of evolutionary processes requires a search for both ancestral patterns and the way these patterns have changed in the course of evolution. This quest for ancestral patterns used either characters or taxa. In the past, taxa which were assessed as exhibiting some

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ancestral characters were misleadingly considered as representing wholly ancestral taxa and were thus named primitive taxa, missing links, living ancestors, forerunners, lower taxa, or stem-groups (*e.g.* ELDREDGE, 1987). These taxa were considered as such probably because it seemed intuitively more realistic and more simple from a gradist perspective to use some living taxa as ancestors than to analyze independently the evolution of many different characters. Evolution was often simply traced between two extant taxa, from a so-called "ancestral taxon" to a so-called "evolved taxon", as if ancestor-descendant relationships could be inferred among present day terminals. There are many examples of such kind of statements concerning cockroaches which were misleadingly considered as "primitive" or "ancestral" relative to termites (*e.g.* TILLYARD, 1936; RAU, 1941; WILSON, 1971, 1975).

This way of thinking is especially misleading because it implies, groundlessly, that most characters are primitive in a taxon by correlation with the primitive state of only a few traits under study (DAWKINS, 1987). It precludes any further advances or at least leads to unclear views, in the understanding of evolutionary processes (KUKUK, 1994). It is moreover phylogenetically nonsensical because phylogenetic characters must be considered *a priori independent* of one another and may be assessed *a posteriori* only *relatively* primitive, according to the principle of heterobathmy (HENNIG, 1966). Ancestors can never be reconstituted in their whole and we can only infer their plesiomorphies using optimisation on phylogenetic trees. Their own autapomorphies have disappeared with them during their evolution. Therefore, ancestors cannot be phylogenetically defined and they will remain paraphyletic taxa (ELDREDGE & CRACRAFT, 1980; NELSON, 1970, 1989).

It is such a paraphyletic picture that I intend to reconstitute here, when dealing with the ancestor of *Cryptocercus*. It should be carefully kept in mind that this picture does not represent any real living or extinct organism but is a hypothesis as to the character states that existed in an ancestor together with autapomorphic and forever unknown traits. The prime interest of such a paraphyletic ancestral picture is to provide heuristic indications as to the evolutionary paths which have led to the present day situation in extant taxa. The woodroach *Cryptocercus* (Fig. 1a) has, since the study of CLEVELAND *et al.* (1934), been especially considered a "primitive taxon" or a "missing link" because it shows traits hypothesized as ancestral to termites, especially xylophagy and protozoan symbionts although the actually ancestral origin of these traits remains controversial (THORNE, 1990, 1991; NALEPA, 1991). This opinion has been discarded by GRANDCOLAS & DELEPORTE (1992, 1996) and GRANDCOLAS (1994a, 1994b, 1995a, 1996a) on the basis of the phylogenetic position of *Cryptocercus*. This position has, hitherto, not been evaluated using modern phylogenetic methodology, and both a reappraisal of and search for characters and their cladistic treatment were obviously needed (DELEPORTE, 1988; GRANDCOLAS, 1994a, 1996a; GÄDE *et al.*, 1997). *Cryptocercus* cannot be a "primitive taxon"

FIG. 1. — Some Polyphaginae and their habitats. **a:** *Cryptocercus punctulatus* female with two young nymphs in the background, in their wood chamber. **b:** *Therea petiveriana* female (bearing an ootheca). **c:** *Ergaula capensis* male and female (bearing an ootheca). **d:** treehole (*Desbordesia glaucescens*) with a termite nest sheltering *E. capensis* in Gabon. **e:** *Heterogamisca chopardi* female (bearing an ootheca). **f:** cushion shrub of *Salsola* sp. beneath which *H. chopardi* burrows, in Saudi Arabia.


a
b
c
d
e
f

because "primitive taxa" cannot be identified, and, according to its phylogenetic position within the Polyphaginae (Fig. 2), its xylophagy and its intestinal symbiosis must be assumed convergent with those of the so-called "lower termites" (GRANDCOLAS, 1995a, 1996a; GRANDCOLAS & DELEPORTE, 1992, 1996). *Cryptocercus* remains however a useful model for understanding and predicting by analogy what could have been the first stages of sociality in termites, relatively to xylophagy and protozoa symbiosis, if one is convinced that these latter traits are ancestral to termites and have determined their evolution toward eusociality (*e.g.* MYLES, 1988; THORNE, 1990; ROISIN, 1994). By the way, it should be kept in mind that this latter hypothesis has not been tested by termite phylogenetic analyses.

Cryptocercus as a member of the subfamily Polyphaginae (Fig. 1) is also an interesting model to study the origin and evolution of a complex subsocial behavior in Insects: *Cryptocercus* defends a wood chamber, feeds its nymphs and transfers to them protozoan symbionts via proctodeal trophallaxis. In this paper, I examine the ancestral states of morphological, anatomical and behavioral traits of *Cryptocercus* involved in its subsocial behavior and in its potentially related behaviors such as habitat use and anti-predator behavior. These states are inferred in reference to the best supported phylogenetic hypotheses concerning *Cryptocercus* and its relatives (Fig. 2).

MATERIAL AND METHODS

Phylogenetic reference. Ancestral states for Polyphaginae and the corresponding derived states in *Cryptocercus* are inferred according to current phylogenetic reconstructions (GRANDCOLAS & DELEPORTE, 1992; GRANDCOLAS, 1994a, 1996a). Cockroach phylogenies are reviewed by GRANDCOLAS (1997a). GRANDCOLAS (1994a) presented a tree of the subfamily Polyphaginae (16 taxa, 50 characters, CI = 0.79 , RI = 0.87) which is used here. Phylogenetic analyses based on RNA and DNA sequences (VAWTER, 1991; KAMBHAMPATI, 1995, 1996) are not taken into account, because they used too small sequenced portions of respectively only 2 and 25 cockroach genera (belonging to a few subfamilies) and no or few genera of Polyphagidae except *Cryptocercus*. Their results were internally inconsistent and moreover incongruent with each other and with both previous systematic concepts (PRINCIS, 1960; MCKITTRICK, 1964) and later morpho-anatomical phylogenetic analyses (GRANDCOLAS, 1996a). KLASS (1995) presented a tree for Isoptera, Blattodea and Mantodea on the basis of the study of 14 species; however, it was not constructed according to a genuine phylogenetic analysis (no matrix of characters, no outgroups, polymorphic characters not coded as such, etc.) and cannot be taken into consideration. According to all these considerations, GRANDCOLAS' (1994) tree is preferred to others for making evolutionary inferences because it has been obtained according to a much more extensive range of taxa and characters, and has a much higher consistency. Moreover, it has received support from the analysis of hypertrehalosaemic neuropeptides from corpora cardiaca (GÄDE *et al.*, 1997). This does not preclude re-examination of results discussed here in the framework of a total evidence approach (KLUGE, 1989).

Attribute optimization on the tree. None of the traits considered in this study were used in tree construction, except when mentioned. Only those supported by primary homology (DE PINNA, 1992) were used to build the tree (see GRANDCOLAS, 1994). Extrinsic (*e.g.* geographical distributions) or poorly defined (*e.g.* social systems) traits are parsimoniously optimized on the tree (as unordered states using Wagner parsimony, FARRIS, 1970), and are treated such as attributes (*sensu* MICKEVICH & WELLER, 1990; GRANDCOLAS *et al.*, 1994). This is in agreement with the principle of total evidence (KLUGE, 1989), which should be applied only to primarily homologous traits (GRANDCOLAS *et al.*, 1994). The ancestral states of these different traits are commented upon here with respect to *Cryptocercus* if they are synapomorphic of [*Therea* + *Cryptocercus*] (the states immediately ancestral to the three described species of *Cryptocercus* are not mentioned as such).

Eight traits were selected. Their states are listed below and in Figures 3-5 and 7-8. The states of these traits have been generalized for each genus on the basis of observations made on different species (Appendix 1). Geographical distributions were established according to taxonomic literature for all described species.

Patterns of geographical distribution (Fig. 3). The analysis of this trait was restricted to the clarification of the ancestral state of [*Ergaula* + *Eucorydia* + *Therea* + *Cryptocercus*] (GRANDCOLAS, 1994b). A simple optimization of the different distribution areas has been carried out on this sub-tree, without engaging in controversial methodologies of phylogenetic biogeography.

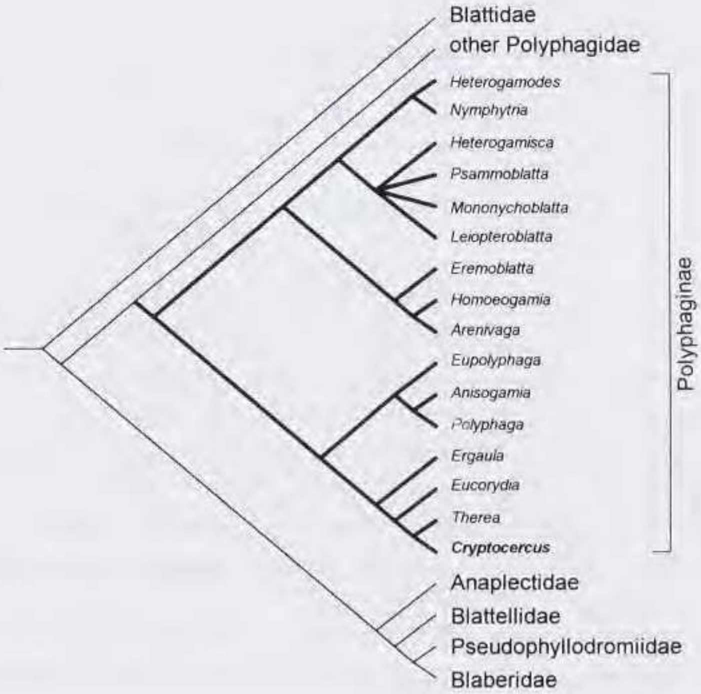

FIG. 2. — A synthetic phylogenetic tree presenting the position of *Cryptocercus* relative to cockroach families, and nested in the subfamily Polyphaginae, according to the analyses of GRANDCOLAS (1994a, 1996a).

Biome occupancy (Fig. 4). Five biomes or combinations of biomes are defined. "Temperate forest + desert" are considered as a single state and not as a polymorphism involving "temperate forest" and "desert" because the species displaying this state are distributed in all these biomes. Tropical forests include both rain and dry forests.

Habitat use (Fig. 5). Six habitats are distinguished from ecological studies (CHOPARD, 1938, 1969; COHEN & COHEN, 1976; EDNEY *et al.*, 1974; GHABBOUR *et al.*, 1977; GRANDCOLAS 1994c, 1995a, 1995b, 1996b, 1997b, HAWKE & FARLEY, 1973; KAPLIN, 1996a, 1996b; LIVINGSTONE & RAMANI, 1978; NALEPA, 1984, 1988a, 1988b; ROTH & WILLIS, 1960; SEELINGER & SEELINGER, 1983; pers. obs.). "Caves or burrows" and "treeholes or termite nests" (Fig. 1f) are not polymorphic characters, because some species inhabit both habitats depending on their relative availability. These habitats are combined as the same state because they are assumed to be similar and to indicate the choice of similar specific physical conditions, namely a cavity underground for "caves or burrows" or a cavity in a biotic structure for "treeholes or termite nests". Cockroaches inhabiting "sand beneath cushion shrubs" (*e.g.* Fig. 1d) do not burrow in "loose sand" and conversely.

Social behavior (Figs 6-7). Three different behaviors may be characterized, according to the classical definitions of MICHENER (1969) revised by EICKWORT (1981): solitary, gregarious and subsocial behaviors. In gregarious species (Fig. 6), larvae and/or adults aggregate independently of relatedness (characteristics of genera according to the same studies as for habitat use). Subsocial species exhibit parental care for the larvae which remain close to their parents. In solitary species, cockroaches never aggregate, even when environmental conditions could force them to be close together. A discussion concerning these traits and their evolution in cockroaches may be found in GRANDCOLAS (1997c).

Anti-predator behavior (Fig. 8). This behavior was coded using three different states: burrowing and freezing (in a loose substratum), disruptive alarm (using presumably disruptive coloration of fore wings with yellow spots and pleural glands, both traits used as characters in GRANDCOLAS, 1994a), and tremulation and obstruction (of galleries) (LIVINGSTONE & RAMANI, 1978; RITTER, 1964; SEELINGER & SEELINGER, 1983; FARINE & BROSSUT, pers. com.; pers. obs.). During disruptive alarm behavior, adult cockroaches raise their wings and exert their pleural glands while larvae rapidly burrowed in the substratum. Wing coloration (Fig. 1b) and movements are assumed to disturb predators and to provoke confusion effects (perhaps not to warn them because gland products are not proved yet to be deterrent). Pleural glands are assumed to produce alarm pheromones and/or allomones (BROSSUT & SRENG, 1985). However, in the laboratory, pleural glands are also exerted

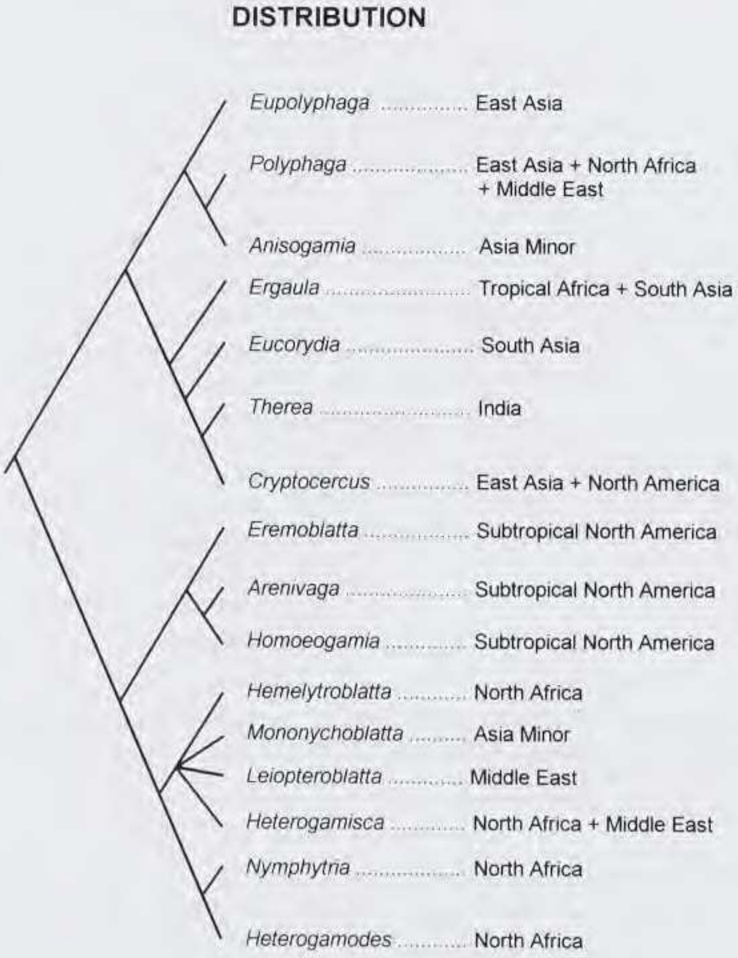

FIG. 3. — Distribution of the genera of the subfamily Polyphaginae.

during conspecific encounters, indicating that pleural glands may also assume other roles such as social or sexual communication (BROSSUT & FARINE, pers. com.). The disruptive alarm behavior may vary: some *Ergaula* species lack disruptive coloration on the wings but they have pleural glands and are able to exert them (*E. capensis* in Gabon, GRANDCOLAS, 1997b).

Ootheca laying behavior. The Polyphaginae either lay their oothecae within the substratum without gluing or coating, or they bury them (GHABBOUR *et al.*, 1977; GRANDCOLAS, 1994c; 1995a, 1996b, 1997b, pers. obs.; KAPLIN, 1996b; MCKITTRICK, 1964; NALEPA, 1988a).

Diet and intestinal symbiosis. In addition, these two attributes were taken into consideration but were not described in detail here because they have been studied previously (GRANDCOLAS, 1995a; GRANDCOLAS & DELEPORTE, 1996). Both have two states: xylophagous diet (in *Cryptocercus*) versus saprophagous diet and presence of flagellate intestinal symbionts (in *Cryptocercus*) versus absence.

Estimates of the derivative loads (BRINCK, 1977; ANDERSEN, 1979) were provided for each node inside the phylogenetic tree of the subfamily Polyphaginae to which *Cryptocercus* belongs. Derivative loads represent the number of derived characters in a taxon or at a node, relative to the total number of characters in the tree; these loads may be considered estimates of the amount of evolutionary change that has occurred at each step in the diversification of a group. These derivative loads are estimated using the tree of GRANDCOLAS (1994a), with addition of autapomophic characters taken from other publications (GRANDCOLAS, 1993; 1994c) or from observations listed in Appendix 2. These estimates are obviously very imprecise since they are based on a relatively small sample of characters. They must not be considered as indicative of true evolutionary rates since they are free of clock assumptions (time periods are not assumed identical between nodes in cladistic trees).

RESULTS

Most parsimonious phylogenetic patterns

The optimization of traits on the phylogeny are shown in Figures 4-5 and 7-8. All equally parsimonious patterns are shown in the figures; the differences between these patterns do not influence the conclusions concerning the ancestor of *Cryptocercus*. According to these optimizations, 8 characters' states are listed for the ancestor of *Cryptocercus* (Table 1).

Distributional patterns (Fig. 3). Using a hypothesis of modification of an ancestral area by vicariance, [India + South Asia + East Asia] is inferred to be the ancestral area of the monophyletic group [*Ergaula, Therea, Eucorydia, Cryptocercus*], with secondary presumptive dispersals into tropical Africa (in the lineage leading to *Ergaula capensis*), and into North America (in the lineage leading to *Cryptocercus punctulatus*). Using the phylogenetic pattern, the ancestor of *Cryptocercus* is hypothesized to have been distributed in Indo-Asia.

Biome occupancy (Fig. 4). Two patterns implying four steps are equally parsimonious. They differ by changes in the group [*Eupolyphaga, Polyphaga, Anisogamia*]: either "temperate forest + desert" is ancestral to this group with a change to "desert" in *Anisogamia*, or "temperate forest + desert" appeared convergently in *Eupolyphaga* and *Polyphaga*. The subfamily originated in deserts and secondarily occupied tropical forests (ancestor of [*Ergaula + Therea + Eucorydia + Cryptocercus*]) and then invaded temperate forests (*Cryptocercus*). The ancestor of *Cryptocercus* was thus distributed in tropical forests.

TABLE 1. — Characters'state of the ancestor of *Cryptocercus*, determined according to the optimizations on the phylogeny of the subfamily Polyphaginae. Optimizations of diet and intestinal symbiosis are given according to GRANDCOLAS (1995a) and GRANDCOLAS & DELEPORTE (1996).

Character	Ancestral state
Distribution	India + Asia
Biome	Tropical forests
Habitat	Treeholes or holes in termite nests
Social behavior	Gregariousness
Alarm behavior	Yellow spots on wings and pleural glands
Diet and intestinal symbiosis	Saprophagy and lack of intestinal Protozoa
Ootheca laying behavior	Without care

Habitat (Fig. 5). Two patterns implying eight steps are equally parsimonious. They involve the ancestral habitat "loose sand" for the subfamily, with either a change to "caves or

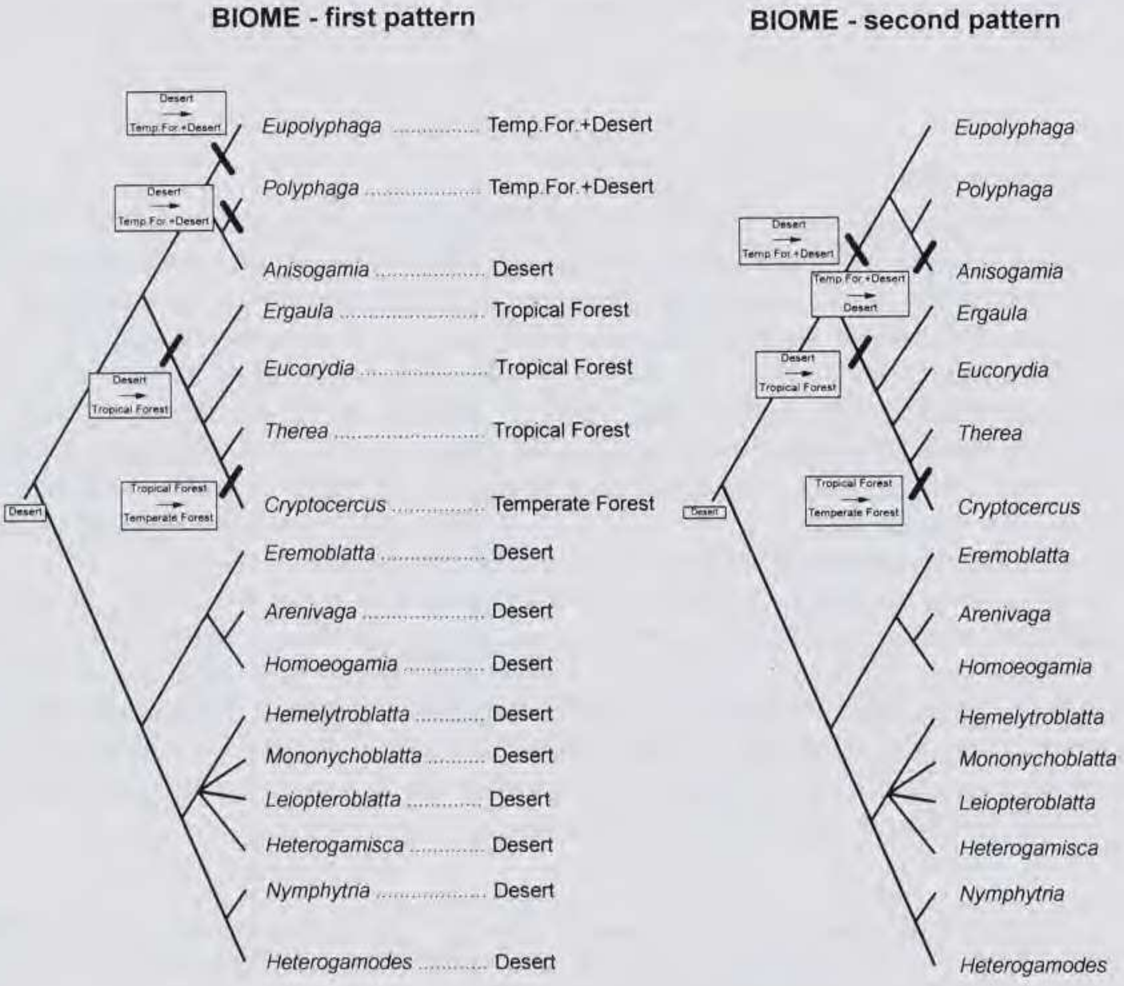

FIG. 4. — Two most parsimonious patterns for the evolution of biome occupancy on the phylogenetic tree of the subfamily Polyphaginae. The state changes are indicated on the branches where they take place.

burrows" in the ancestor of [*Arenivaga* + *Homoeogamia*] with a subsequent reversal to "loose sand" in some species of *Arenivaga*, or two changes toward "caves or burrows" in *Homoeogamia* and some *Arenivaga*. In either case, there was a shift toward "treeholes or termite nests" in the ancestor of [*Ergaula* + *Therea* + *Eucorydia* + *Cryptocercus*]. Some species of *Therea* secondarily changed and inhabited "ground litter" and *Cryptocercus* switched to "rotten trunk". The ancestor of *Cryptocercus* inhabited cavities such as treeholes or termite nest holes.

Social behavior (Fig. 7). The ancestor of Polyphaginae was gregarious with two reversals toward solitariness occurred in species belonging to the genera *Heterogamisca* and

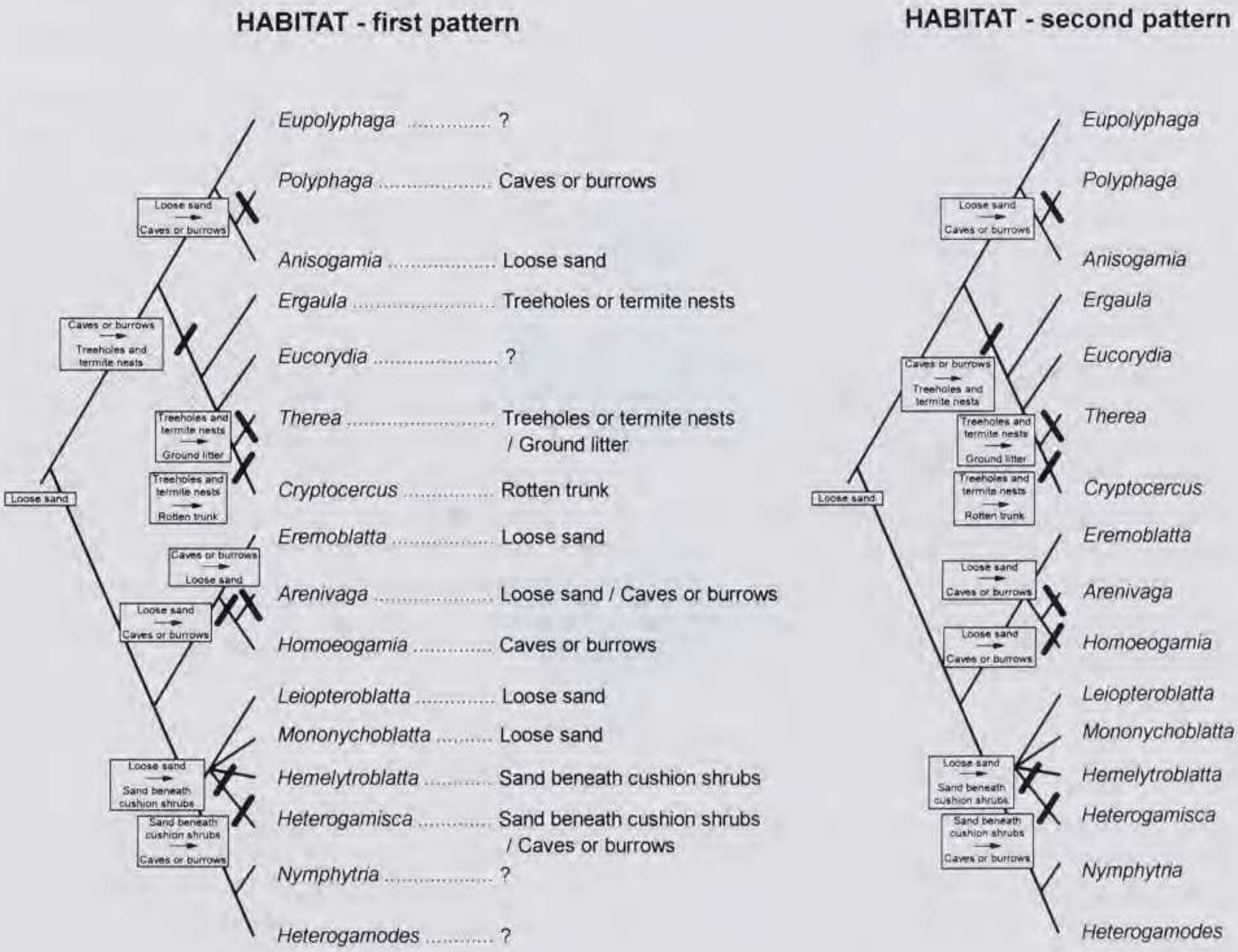

FIG. 5. — Two most parsimonious patterns for the evolution of habitat use, implying the habitat "loose sand" as an ancestral state. Question marks indicate unknown states of attributes.

Arenivaga. Subsociality (familial brood care) appeared in *Cryptocercus*. Its ancestor was thus gregarious.

Anti-predator behavior (Fig. 8). According to the most parsimonious pattern, the ancestor of Polyphaginae showed "burrowing and freezing" as an anti-predator behavior. Disruptive alarm is ancestral to [*Ergaula* + *Therea* + *Eucorydia* + *Cryptocercus*]. Even though this state is partly inapplicable in the totally apterous *Cryptocercus* (for wing coloration), its ancestor may be inferred to have had disruptive alarm. Pheromonal pleural glands and disruptive coloration of wings (Fig. 1b) appeared in the ancestor of [*Ergaula* + *Therea* + *Eucorydia* + *Cryptocercus*] and disappeared in *Cryptocercus* which acquired a particular alarm behavior, combining tremulation in nymphs and defense of the chamber entrance by adults (gallery obstruction with pronotum).

Source : MNHN, Paris

Oothecal laying behavior. All observed species of Polyphaginae deposit their oothecae in the substratum without any coating or gluing, except *Cryptocercus*. *C. punctulatus* was observed to burrow a hole in dead wood, to deposit its ootheca inside and then to enclose it (McKittrick, 1964). The ancestor of *Cryptocercus* deposited its ootheca without care.

Most of the changes occurring according to these parsimonious scenarios are combined to define an overall evolutionary scenario comprising several evolutionary paths (Fig. 10): either gregarious ancestors in Polyphaginae have changed their biomes and remained gregarious or they have remained in the ancestral biome and changed their social behavior. Gregarious ancestors living in a derived biome have also evolved toward subsociality.

Derivative loads

Autapomorphies of terminal taxa are listed in Appendix 2. Together with synapomorphies, there are 108 characters. Loads are provided for each node of the cladogram (Fig. 9). The most important loads for present discussion are present in the monophyletic group comprising *Ergaula*, *Eucorydia*, *Therea* and *Cryptocercus*. The genera *Cryptocercus, Therea, Eucorydia* have especially high derivative loads, which are at least twice the mean value of other taxa (respectively 31.5 %, 24.1% and 25% relative to 9.5% as the mean). The difference between *Cryptocercus* and its common ancestor with *Therea* is also the highest value recorded at a node (12.1%). Clearly, among the set of characters examined, the amount of evolutionary change increases as one gets closer and closer to *Cryptocercus*.

DISCUSSION

The ecological and behavioral ancestral attributes of Cryptocercus

Although it was never placed as the nearest relative of termites in any taxonomic or phylogenetic scheme (*e.g.* HENNIG, 1981; THORNE & CARPENTER, 1992; see also KRISTENSEN, 1995), *Cryptocercus* has been considered to have a way of life ancestral to cockroaches and termites solely because of its xylophagy, protozoan symbionts and familial way of life (CLEVELAND *et al.*, 1934; GRASSÉ & NOIROT, 1959; WILSON, 1971; NALEPA, 1984, 1991, 1994; MYLES, 1988). Nonetheless, according to phylogenetic analysis (GRANDCOLAS, 1994a, 1996a) all these traits are actually apomorphic to *Cryptocercus*. This does not support the hypothesis that *Cryptocercus* inherited these traits from a common ancestor with termites but supports the hypothesis of origin of these traits by convergence (xylophagy, social system) and transfer (symbionts)(GRANDCOLAS & DELEPORTE, 1992, 1996; GRANDCOLAS, 1994b, 1995a, 1996a). According to these statements, *Cryptocercus* and other subsocial cockroaches do not deserve thus to be compared with termites in a *strict* phylogenetic perspective (*contra* CRESPI, 1996).

Xylophagy, protozoan symbionts, and familial way of life were so firmly considered as ancestral to cockroaches and termites that their origin was never questioned. Also, the origin of subsocial behavior was poorly investigated in insects using phylogenetic comparative biology because of the lack of phylogenies. Using the phylogeny, it is possible to infer that the ancestor of *Cryptocercus* was distributed in tropical forests of Indo-Asia, and inhabited treeholes and/or holes in termite nests (Fig. 10). It was gregarious: larvae were clumped in the same cavity, often together with some adults which were not necessarily their parents. These adults laid their oothecae without care in the loose litter at the bottom of cavities. The ancestors of *Cryptocercus*

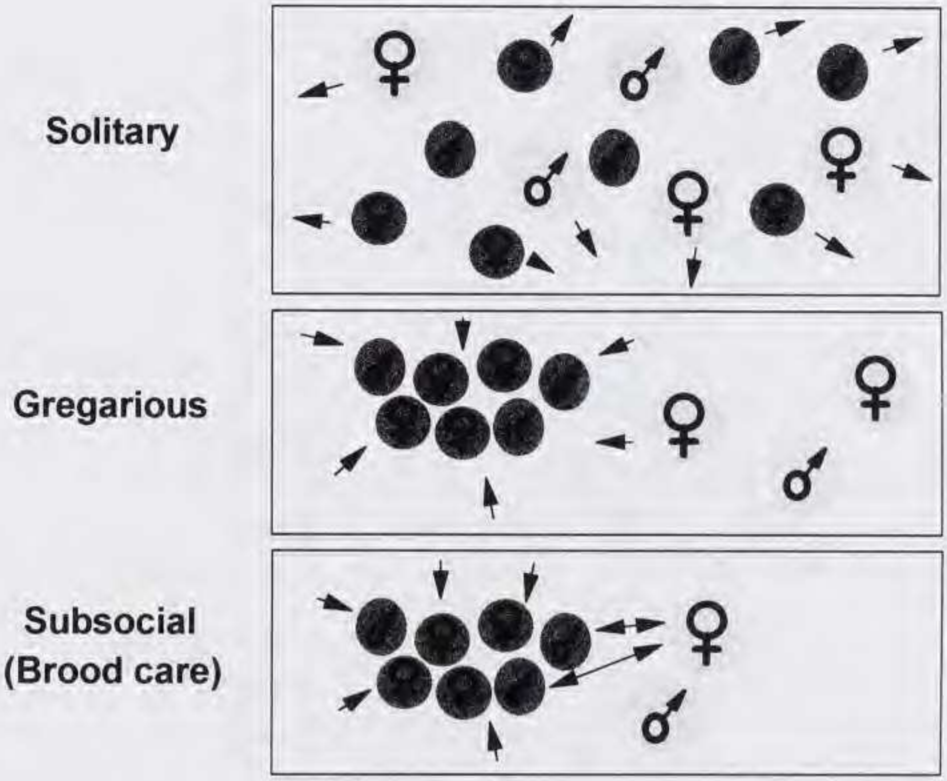

FIG. 6. — A simplified representation of cockroach social systems involving adults (large and light grey circles) and larvae (small and dark grey circles), their interactions cohesive (arrows directed inward), or dispersive (arrows directed outward), and brood care (double arrows).

displayed a disruptive alarm behavior (raising fore wings with yellow spots and exerting pheromonal pleural glands). There were many important evolutionary changes from these ancestors since most of these character states were modified to account for the very different present aspect and behavior of *Cryptocercus*. Derivative loads are especially high in the part of the cladogram close to *Cryptocercus* and increase sequentially at the dichotomies leading to [*Ergaula* + *Eucorydia* + *Therea* + *Cryptocercus*], [*Eucorydia* + *Therea* + *Cryptocercus*] and [*Therea* + *Cryptocercus*]. Indeed, most of the characters sampled for phylogenetic studies change close to *Cryptocercus*, including its divergence from the common ancestor with its sister-group *Therea*. From a gregarious ancestor, inhabiting cavities (*e.g.* Fig. 1d) and showing a disruptive coloration, evolution produced a descendant which was subsocial, digging into the wood, lacking wings and strongly armored. Unfortunately, most changes concerning biome, habitat, social system and alarm behavior occurred at the same node of the cladogram and it is thus impossible to assess the relative sequence of these different events using my phylogenetic hypothesis (Figs 4, 5, 7, 8). By analogy with the diversification of the subfamily Zetoborinae in South America, it is possible that the xylophagy of *Cryptocercus* appeared before it dispersed

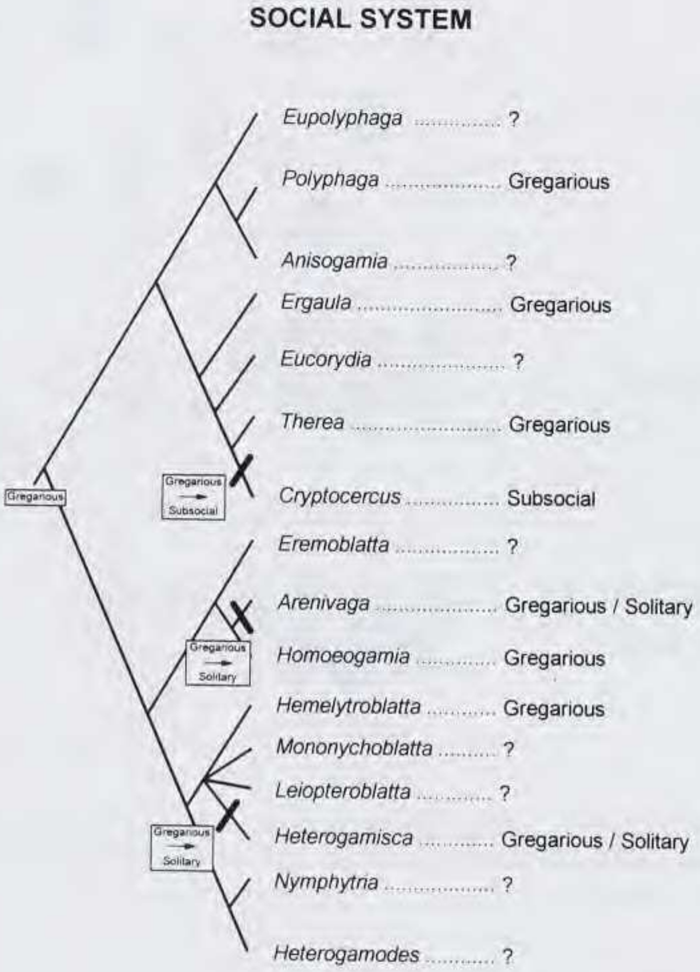

FIG. 7. — Most parsimonious pattern for the evolution of social system.

to temperate forests because a wood diet and its life history correlates could facilitate adaptation to a seasonal temperate climate (see GRANDCOLAS, 1995a for an evolutionary scenario linking wood diet and adaptation to climate). It is necessary however to get additional data (*e.g.* still unknown tropical *Cryptocercus* species or relatives) to substantiate this hypothesis in the present case of the subfamily Polyphaginae.

The alarm behavior changed together with social system, but the different alarm behaviors displayed by gregarious and subsocial taxa require a high degree of behavioral coordination among conspecifics (so-called "cooperation" according to WILSON, 1975). This coordination could be related to behavior of cooperative groups (MILINSKI, 1979). They seem thus to be identical in this respect. Alarm behavior appeared each time to cope with communication constraints imposed by each kind of habitat. Species living in large cavities (Fig. 1d)

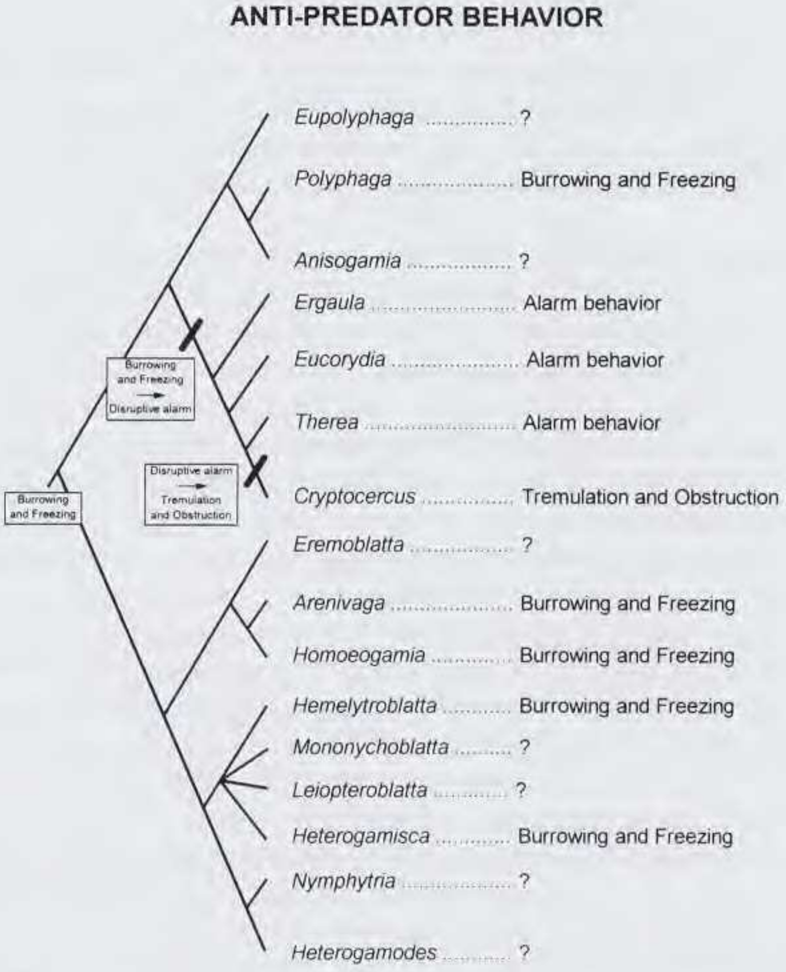

FIG. 8. — Most parsimonious pattern for the evolution of anti-predator behavior.

or in ground litter (the ancestor of *Cryptocercus* and *Therea* and *Ergaula* species) displayed a disruptive coloration (Fig. 1b), an alarm or repugnatory gland and a burrowing ability. This could protect them against large predators using visual perception (presumably vertebrates). Species living in small obscure chambers in rotten trunks displayed tremulation and gallery obstruction. This could protect them against small predators detecting their prey with help of vibrations and odors (such as millipedes, spiders, etc., see MATSUMOTO, 1992 for depicting such predation events in similar cockroaches belonging to the subfamily Panesthiinae). Tremulation in an obscure cavity provides other members of the family with alarm: larvae clump beneath the female who may close the gallery with her body (SEELINGER & SEELINGER, 1983).

From gregariousness to subsociality: an overlooked path

Most recent evolutionary theories regarded subsociality as a step toward eusociality. Parental care (central to the concept of subsociality) is a standard principle of a kinship-based understanding of social evolution (*e.g.* NALEPA, 1994; TALLAMY, 1986). Gregariousness and parasociality are often considered as more or less blind alleys, resulting from similar natural selection pressures to those exerted during the evolution of subsociality (*via* anti-predation, foraging, etc.) but failing in this case to lead to more complex or integrated forms of sociality because of the lack of kinship between the members of the gregarious groups (WILSON, 1971, 1975).

In the subfamily Polyphaginae, a presocial behavior – gregariousness – clearly preceded the appearance of subsocial behavior in *Cryptocercus* (Fig. 10). What could be the significance of such a pattern? Could presociality be exaptive (*i.e* preadaptive) for subsociality? This kind of prospect is a process-oriented question and deals with models of selection whereas phylogenies depict evolutionary pattern. In this way, it could be hypothesized that both tolerance to conspecifics and behavioral coordination may be selected in a context of gregariousness and may be highly exaptive in a subsocial context. Tolerance to crowding and interattraction are the first (pre-)requisites of social relationships (ALLEE *et al.*, 1949; GRASSÉ, 1952), as revisited recently by CRESPI (1994). Both tolerance and interattraction could be first acquired during the evolution of gregarious life. In gregarious species, individuals cluster together because they are interattracted together. Living in aggregations, they must tolerate spatial proximity with their conspecifics and do not spend time or waste energy in aggressive or dispersive behaviors. Both tolerance and interattraction could be inherited in subsocial descendants where they could have an exaptive value because subsocial mother and larvae are closely associated and have mutual interactions which necessitate both behaviors. The only difference between gregarious and subsocial species could be the propensity of individuals to show tolerance and attraction toward different kind of conspecifics, respectively in the context of non-kin individuals or in the context of a family. In the same way, the alarm behavior of gregarious ancestors could be mediated by the reactivity to movements of non-kin conspecifics via specialized mechanical receptors. This reactivity as well as these receptors could have been inherited by their subsocial descendants and have a high selective value when displayed with kin conspecifics during their own alarm behavior. An efficient alarm behavior has, by itself, a high selective value because it allows individuals to escape death or injury by predators or parasites. All the alarm behaviors described in the Polyphaginae were displayed through communication within some groups of individuals. In the same way as for social system, the sensory and neurological basis for this communication may be selected first in one context (between non-kin) and then used secondarily in a somewhat different context (between kin). According to this possible exaptive value of gregariousness toward subsociality, a possible path for the appearance and change of social system could be traced from gregariousness to subsociality, and possibly to eusociality by *analogy* to termites. This hypothesis of exaptive value of gregariousness toward subsociality is quite different from the statements that parental care seems to be more frequent in ovoviparous taxa or in oviparous taxa carrying oothecae a long time than in most oviparous. GRANDCOLAS (1996) and NALEPA & BELL (1997) independently reported this trend respectively in reference to a phylogenetic hypothesis and to a traditional classification, respectively. Ovoviviparity or long-carrying of

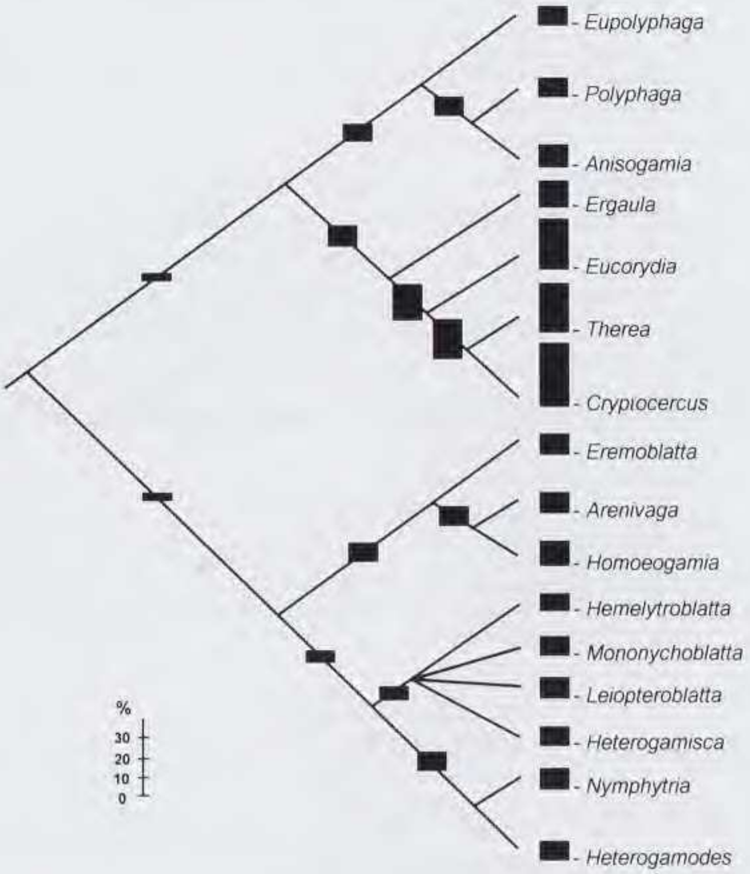

FIG. 9. — Derivative loads (ratios of apomorphies relative to the subfamily groundplan sampled with 108 characters) indicated on the phylogenetic tree of the subfamily Polyphaginae.

oothecae are supposed by both papers – at least among several factors – to increase and promote the relationships between the female and the larvae which are necessarily close following the brood birth. These statements did not imply necessarily that gregariousness is ancestral and exaptive to parental care but merely that particular reproductive mode or more generally life history may promote parental care.

Insights by analogy concerning the evolution of termites

Evolutionary inferences concerning the appearance of sociality in termites have always considered the prominent role of subsociality (parental care) in xylophagous ancestors. Ancestors were hypothesized to be xylophagous and to harbor intestinal symbionts (CLEVELAND *et al.*, 1934; GRASSÉ & NOIROT, 1959). This symbiosis would have determined a subsequent evolution toward parental care which is needed for transferring symbionts (*via* proctodeal trophallaxis between mother and larvae). This care for young nymphs could have shifted from adults to older nymphs and this could have been responsible for the emergence of a worker caste (NALEPA,

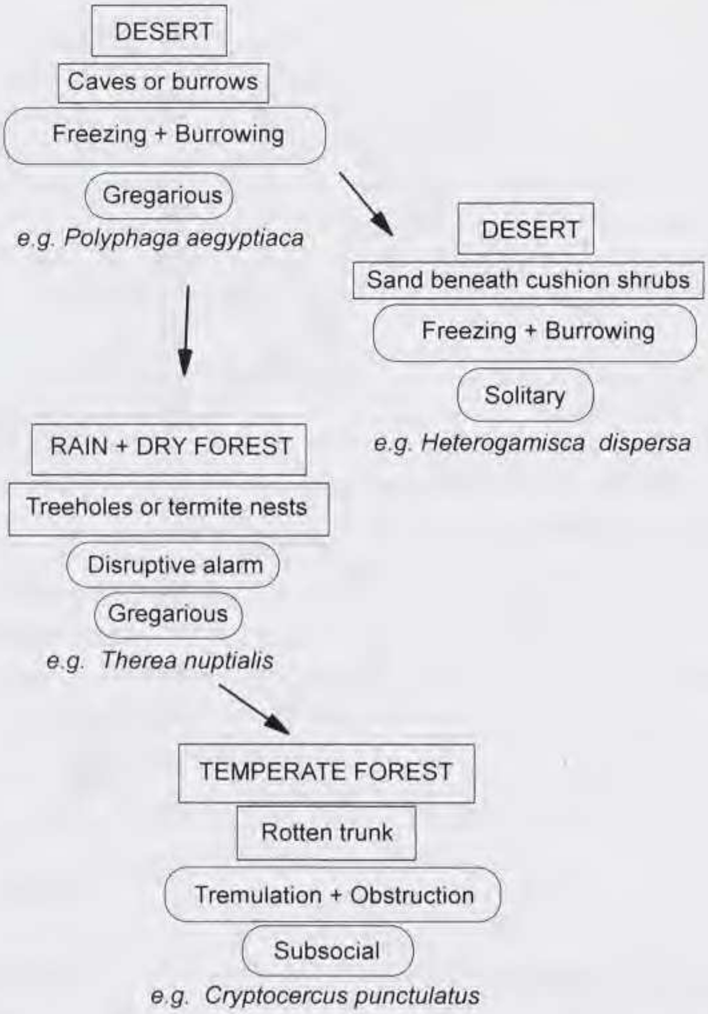

FIG. 10. — Several possible evolutionary paths according to the most parsimonious scenarios concerning biome, habitat and social behavior depicted in the Figures 3, 4 and 6.

1988b, 1994). This scheme is, however, dependent on the assumptions that xylophagy and symbiosis were both ancestral to termites. *Cryptocercus* is unfortunately not useful for testing these assumptions directly *by homology* because it is not closely related to termites (GRANDCOLAS & DELEPORTE, 1992, 1996). However, *by analogy*, the patterns in the clade to which *Cryptocercus* belongs suggest that an ancestor of termites could have exhibited a particular alarm or anti-predator behavior. This behavior could have promoted an evolution toward subsociality as well as symbiosis and parental care. This kind of evolutionary relationship between anti-predator behavior and sociality has already been postulated concerning insects (*e.g.* STARR, 1985; CRESPI, 1994; but see KUKUK *et al.*, 1989). Unfortunately, chemical or other defenses of alates in termites are very poorly known (DELIGNE *et al.*, 1981; GRASSÉ, 1986). The studies of MOORE (1968, 1969) interestingly suggested that many termites (including alates of Mastotermitidae and Termitidae) have mandibular glands with a defensive role (quinone-secreting): a so widely distributed gland could be an indication of an ancestral pattern of defensive behavior similar to that shown in cockroaches. However, there is also few phylogenetic analyses of termites, except a limited molecular attempt (KAMBHAMPATI *et al.*, 1996): additional work is thus needed to understand whether a particular defensive behavior operated in the ancestor of termites.

In conclusion, searching for patterns ancestral to the subsociality of *Cryptocercus* provides useful insights concerning the evolution of sociality. First of all, the previous assumptions of relictual ancestral subsociality associated with xylophagy and intestinal symbiosis as shared ancestrally by *Cryptocercus* and termites are discarded. The ancestors of *Cryptocercus* clearly lacked these traits. Second, gregariousness, subsociality and anti-predator behavior are associated in the same phylogenetic pattern. This pattern may be used to implement current models of social evolution which are too narrowly based on the relationship between parental care and resource use.

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APPENDIX 1. — Species which are used for the generalizations at the generic level of the ecological and behavioral traits under study (information pertaining to each species may be found in the references cited in the material and methods section).

Arenivaga apacha (SAUSSURE, 1893)
A. bolliana (SAUSSURE, 1893)
A. erratica (REHN, 1903)
A. floridensis CAUDELL, 1918
A. investigata FRIAUF & EDNEY, 1969
A. tonkawa HEBARD, 1920
A. sp.
Cryptocercus punctulatus SCUDDER, 1862
C. relictus BEY-BIENKO, 1935
Ergaula capensis (SAUSSURE, 1893)
E. carunculigera (GERSTAECKER, 1861)
E. sp.
Eremoblatta subdiaphana (SCUDDER, 1902)
Eucorydia dasytoides (SAUSSURE, 1864)
E. ornata (SAUSSURE, 1864)
E. westwoodi (GERSTAECKER, 1861)
Hemelytroblatta (=*Psammoblatta*) *africana* (LINNAEUS, 1758)
Heterogamisca chopardi (UVAROV, 1936)
H. dispersa GRANDCOLAS, 1994
H. marmorata (UVAROV, 1936)
Homoeogamia mexicana BURMEISTER, 1838
Leiopteroblatta monodi CHOPARD, 1969
Mononychoblatta semenovi CHOPARD, 1929
Polyphaga aegyptiaca (LINNAEUS, 1758)
P. indica WALKER, 1868
P. pellucida (REDTENBACHER, 1889)
P. saussurei (DOHRN, 1888)
Therea petiveriana (LINNAEUS, 1758)
T. nuptialis (GERSTAECKER, 1861)

APPENDIX 2. — Autapomorphies of different genera of the subfamily Polyphaginae, in addition to those listed in previous publications (GRANDCOLAS, 1993, 1994a, 1994c).

Genus	Autapomorphy
Anisogamia	pronotum impressed on the middle large mesonotum and metanotum (homoplastic with *Leiopteroblatta*) tarsal claws short
Arenivaga	antero-ventral margin of female fore femora with a long row of short and strong spines closely inserted supra-anal plate moderatley lengthened and emarginate
Cryptocercus	pronotal sculpture eyes reduced loss of setae on external sclerites abdominal segment VII expanded intestinal pouch (for flagellates) lack of clypeo-frontal suture wings totally lacking lack of cercal spheroid sensilla (homoplastic with *Eucorydia*) lack of pleural glands hook L3d of male genitalia not at all protruding ventral phallomere in male genitalia leg spines strong inter-tergal glands (FARINE *et al.*, 1989)
Eremoblatta	middle and hind femora without apical spine male subgenital plate very asymmetrical with two lateral projections
Ergaula	third frontal hollow females brachypterous while males macropterous (homoplastic with *Homeogamia*) fronto-clypeal suture invaginated where it joins the median suture
Eucorydia	metallic coloration of pronotum yellow spots on wings reaching the fore margin postclypeus flat hook L3d of male genitalia short lack of cercal spheroid sensilla (homoplastic with *Cryptocercus*) hind tubercle of R2 with a finger-like apophysis neoformation with a projected hind lobe fore tubercle of R2 projected
Eupolyphaga	setae with reddish coloration L3d and L3v enveloping and rounded outer outline of female eyes not rounded dorsally and ventrally
Hemelytroblatta	female subgenital plate with a median constriction
Heterogamisca	hind tibiae curved front flat alongside fronto-clypeal suture anal field of fore wings broad

APPENDIX 2. — continued.

Heterogamodes	small tarsal claws (homoplastic with *Anisogamia*) female pronotum with strongly and regularly convex fore border large tergal glands just below the metanotal hind margin
Homoeogamia	female winged (homoplastic with *Ergaula*, *Eucorydia*, *Therea*) male fore wings with wide and horizontally subcostal field) male pronotum wider on the fore border female subgenital plate with two flaps
Leiopteroblatta	wings short with veins not visible male eyes small one tarsal claw (homoplastic with *Mononychoblatta*) hind femora spatulate and wide antero-ventral carena on middle and hind femora without spines but with long and strong setae small ocelli in males
Mononychoblatta	tarsae with only one claw (homoplastic with *Leiopteroblatta*) large metanotum and mesonotum (homoplastic with *Anisogamia*)
Nymphytria	small pronotum mesonotum laterally large hind femora spatulate only in the apical half lack of tarsal claws in females
Polyphaga	pronotum with white fore margin contrasting with dark coloration (homoplastic partly with *Hemelytroblatta*)
Therea	at least four yellow spots distinctly colored on fore wings fore wings black between yellow spots L2v diameter not increasing L3v posteriorly protruding Neoformation flattened